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Revision of the *Phytomyza syngenesiae* group (Diptera, Agromyzidae), including species hitherto known as "*Phytomyza atricornis* Meigen"

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With 23 Figures

I. Introduction 1
II. The *Phytomyza syngenesiae* group 2
III. Treatment of species 4
IV. Notes on types and nomenclature 19
V. Relationship of the *Phytomyza syngenesiae* group with other species of *Phytomyza* 22
VI. Discussion of evolutionary problems 23
VII. Acknowledgements 25
VIII. Summary 26
IX. References 26

I. Introduction

The small group of species treated in this paper includes two species, *Phytomyza syngenesiae* (Hardy) and *P. horticola* Goureau, which are of substantial economic importance. Hitherto these species have been confused in the literature, since they are not separable on the basis of external morphology. On present knowledge a reliable diagnosis is possible only by examination of the male aedeagus. Dissection of the abdomen is necessary for this examination, except in the case of specimens whose aedeagus is extruded as during copulation. Since 1920 the above two species have generally been called „*Phytomyza atricornis* Meigen", a name whose use I propose to discontinue for reasons which are explained below in the section headed "Notes on types and nomenclature". An immense literature has accumulated on these two species. I have devoted my attention in this study mainly to taxonomic and biological papers, and have made no attempt to consider papers concerned primarily with control measures.

The figures of male genitalia in this paper are based on specimens which have been cleared in potassium hydroxide or sodium hydroxide, as is the practice in most contemporary work on the Agromyzidae.

The descriptions given in this paper refer solely to characters which seem to me useful for purposes of identification or relevent to the classification proposed. Additional information on the external morphology of the adults can be obtained from the very detailed descriptions of "*Phytomyza atricornis* Meigen" given by Hendel, 1934 (probably based both on *P. syngenesiae* [Hardy] and *P. horticola* Goureau) and Melis (1935), whose paper clearly refers to *P. horticola* Goureau, as is shown by his figures of the male genitalia. Some details of the female genitalia of *horticola* are given by Melis (1935) and Sasakawa (1961 a). Studies of the larval morphology and biology of *horticola* (as "*atricornis*") have been published by Melis (1935), Ahmad and Gupta (1941), Buhr (1953), Kuroda (1960) and Trehan and Sehgal (1963). However the only biological accounts certainly referable to *syngenesiae* are those referring to America (of which the most detailed is that of Smulyan, 1914) and New Zealand (see Watt, 1923 and Kelsey, 1937). The results of the important British studies by Cohen

(1936) and Hussey and Gurney (1962) require clarification, since the identity of the species concerned is not clear. At least the latter used material of two species *(syngenesiae* and *horticola)* in their work, but the details of which species was used in each particular experiment cannot now be reconstructed. Fortunately Dr. Hussey is continuing his work on this subject, and it is to be hoped that he will be able to clarify his earlier results in due course. It is also not clear whether the larval descriptions given by Allen (1958) and de Meijere (1926) relate to *P. syngenesiae* (Hardy) or *P. horticola* Goureau.

Some of the technical terms of phylogenetic systematics used in this paper (such as "apomorph", "plesiomorph" etc.) may perhaps still be unfamiliar to some readers. My use of these terms is in accordance with the definitions proposed in the works of Hennig. A convenient summary of his views has recently appeared in English (Hennig, 1965).

The following abbreviations are used to indicate the location of material recorded in this paper:

AM	The Australian Museum, Sydney
BM	British Museum (Natural History), London
CSIRO	Commonwealth Scientific and Industrial Research Organization, Canberra
DEI	Deutsches Entomologisches Institut, Eberswalde
GCDG	The author's personal collection
GCRI	Glasshouse Crops Research Institute, Littlehampton, Sussex, England
HEL	University Zoological Museum, Helsinki
ISZ	Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität, Berlin
KAS	Mr. K. A. Spencer's collection, London
KB	Universitetets Zoologiske Museum, Copenhagen
LUND	Zoological Institute, University of Lund
MNHN	Muséum National d'Histoire Naturelle, Paris
NMI	National Museum of Ireland, Dublin
USNM	U. S. National Museum, Washington
WIEN	Naturhistorisches Museum, Vienna

Other abbreviations used in recording material are:

ex.	examples
em.	emerged
leg.	legit (i. e. collected)

I have stated the collector's name, where known, for all material collected by workers other than myself.

II. The *Phytomyza syngenesiae* group

General Description

Adult

External Morphology: Head (fig. 1) with the orbits not or only narrowly projecting above the eye in lateral view. Two upper orbital bristles *(ors)* of about equal length present, but only a single strong lower orbital *(ori)* except sometimes in *aragonensis*. Third antennal segment short and rounded. Eye distinctly higher than long (contrast *Phytomyza plantaginis* Robineau-Desvoidy), with only very sparse pubescence (contrast *P. nigra* Meigen).

Acrostichal hairs sparse (at most six to seven present in *farfarella* and *lindbergi*) or completely absent (in *aragonensis* and most specimens of *syngenesiae* and *horticola*): intra-alar hairs very few, usually only one or two presuturals present (occasionally there is also a single postsutural, but usually this is absent).

Wing (fig. 2) with the second costal segment (between the apices of r_1 and r_{2+3}) $1^1/_2$—2 times as long as the fourth segment (between r_{4+5} and m_{1+2}).

Colour: Frons entirely yellow or occasionally with the upper part of the orbits slightly darkened. Face yellow, with a variable degree of infuscation in the hollows below the antennae. Antennae largely dark, at most with the first and second segments yellow-brown. Thorax almost entirely matt grey, with only the wing base and dorsal

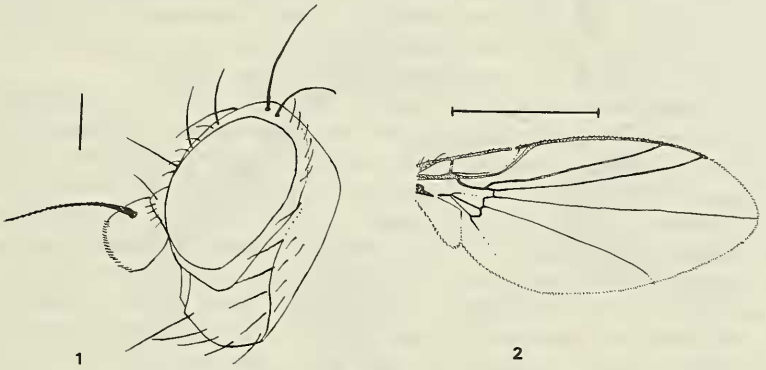


Fig. 1. Head in lateral view of *Phytomyza syngenesiae* (Hardy). (Scale 0.1 mm.)
Fig. 2. Wing of *Phytomyza syngenesiae* (Hardy). (Scale 1 mm.)

margin of the mesopleuron yellow. Femora largely dark, with yellow apices. Basal cone of ovipositor (♀) entirely grey dusted *(aragonensis)*, or grey dusted basally but with its apical half or third shining *(farfarella, syngenesiae* and *horticola)*.

Size small (wing length not exceeding 2.6 mm).

♂ genitalia: Surstylus (fig. 20) with a small group of hairs at its tip, only partially fused with the epandrium (9th tergite), delimited by a distinct suture on its outer side. Aedeagus (figs. 5, 7—9, 12, 13, 16, 17 and 21) with the basiphallus consisting of two long sclerites which diverge apically; mesophallus forming a characteristic elongate tubule; distiphallus arising from the base of the mesophallus. Ejaculatory bulb (fig. 6, 11, 15 and 19) relatively small.

♀ genitalia: Spermathecae minute and orbicular (see Sasakawa, 1961 a).

Larva

Mouthparts and cephalopharyngeal skeleton as in the majority of *Phytomyza* spp. Mandibles each with two alternating teeth, the right mandible being longer than the left. Spiracles (both front and hind) small, with 6—12 bulbs.

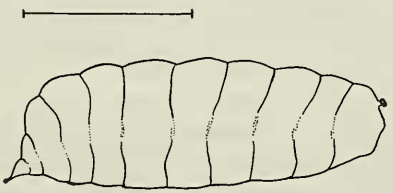


Fig. 3. Puparium of *Phytomyza syngenesiae* (Hardy). (Scale 1 mm.)

Biology

The larvae form linear mines in the leaves of various herbaceous plants, pupating within the leaf in a "pupal blister". The puparium (fig. 3) lies with its ventral surface adjacent to the surface of the leaf, with its front spiracles projecting ventrally through the epidermis.

The *Phytomyza syngenesiae* group as here conceived is well characterised as a monophyletic group by the form of the aedeagus, particularly the characteristic elongate form of the mesophallus. This is an apomorph (derivative) character not shown by other species of *Phytomyza*. Other clearly apomorph features of the group are the reduced number of acrostichal and intra-alar hairs, and the low ratio of costal segments 2 to 4. Each of these features however occurs in certain other species of *Phytomyza*, and it is not yet possible to judge whether they characterise the *syngenesiae* group as such, or indicate its synapomorphy with other species.

All adult males and some adult females of the species of the *Phytomyza syngenesiae* group may be distinguished by the key given below. On present information the females of *syngenesiae* and *horticola* cannot be reliably separated; and although many females of *farfarella* can be recognised by their relatively numerous acrostichal hairs, their range of variation in this respect overlaps with that of *syngenesiae*. Considerable caution is thus needed in any attempt to identify isolated females, and it must be accepted that in many cases an identification to species will not be possible. Larvae and puparia were available to me for only three species, *aragonensis*, *syngenesiae* and *horticola;* these do not seem to exhibit any characters suitable for individual diagnosis, though I have little doubt that future studies will reveal statistical differences.

Key to adults of the *Phytomyza syngenesiae* group

1 3rd antennal segment (fig. 4) with a fringe of conspicuous long white pubescence. Acrostichal hairs completely absent. Aedeagus (♂) as fig. 5 . *P. aragonensis* n. sp.
— Pubescence of 3rd antennal segment short and inconspicuous (fig. 1) . . . 2

2 Trochanters and apex of the front coxae rather bright yellow. Six acrostichal hairs *(acr)* present. Aedeagus (♂) as figs. 7 and 8: sclerites of basiphallus becoming broad and obscurely defined towards their apex; distiphallus weak; mesophallus slightly longer than in other species of this group. (Canary Isles) *P. lindbergi* Spencer
— Trochanters and apex of the front coxae dark, or at most yellow-brown . . . 3

3 Aedeagus (♂) as figs. 16—18 and 21: distiphallus strongly developed, divergent from its base; mesophallus bent upwards only at its apex. Acrostichal hairs usually completely absent . . . . . *P. horticola* Goureau
— Aedeagus (♂) as figs. 9, 10 and 12—14: distiphallus more weakly developed, divergent only towards its apex; mesophallus with about its apical third bent upwards 4

4 Usually four to seven acrostichal hairs present, rarely no more than two. Aedeagus (♂) as fig. 9, with the sclerites of the basiphallus becoming broad and obscurely defined towards their apex; the sac below the mesophallus is large and usually somewhat sclerotised along its hind margins . . . . . *P. farfarella* Hendel
— Acrostichals often completely absent, at most one to four isolated hairs present. Aedeagus (♂) as fig. 12, with the sclerites of the basiphallus more well defined towards their apex; the sac below the mesophallus is smaller and virtually membranous (easily distorted in preserved specimens) . . . *P. syngenesiae* (Hardy)

III. Treatment of species

Phytomyza aragonensis n. sp.

Holotype ♂ in the Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität, Berlin.

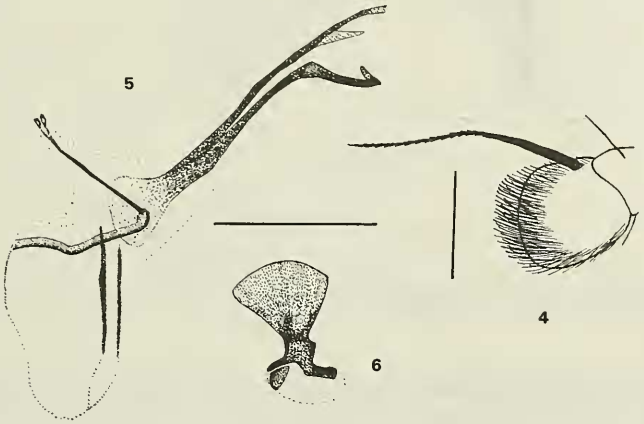
Adult

Development of second lower orbital bristles *(ori)* variable (strongly developed, about half the length of the first *ori*, in the holotype; vestigial in one of the females;

strongly developed on one side only in the other female). 3rd antennal segment (fig. 4) with a fringe of conspicuous long white pubescence.

Acrostichal hairs *(acr)* completely absent.

Trochanters and apex of the front coxae yellow-brown or brown. Basal cone of ovipositor (♀) entirely grey dusted.



Figs. 4—6. *Phytomyza aragonensis* n. sp. holotype ♂: 4, third antennal segment; 5, aedeagus in lateral view; 6, ejaculatory bulb. (Scale 0.1 mm.)

♂ genitalia: Aedeagus (fig. 5) with the distiphallus only weakly divergent towards its apex; mesophallus with its apical third characteristically sinuate; the sac below the mesophallus is large (similar to that of *farfarella)*, with its hind margins strongly sclerotised. Ejaculatory bulb (fig. 6) only weakly asymmetrical.

Material examined: Holotype ♂; 2 ♀♀ paratypes, from larvae and puparia 2. VI. 33 in leaves of *Lactuca tenerrima,* Albarracin, Aragon, Spain, em. mid-VI. 33, leg. Hering no. 4225 (ISZ).

The type series was recorded as "*Phytomyza atricornis* Meigen" by Hering (1936). They were bred from narrow leaf-mines similar to those of *syngenesiae* and *horticola.* Pupation took place on the underside of the leaf.

It should be noted that the species with very long antennal pubescence occurring on *Lactuca* in North America, *Phytomyza lactuca* Frost, is not referable to the *syngenesiae* group as defined in this paper; nor is the European *P. ciliata* Hendel (associated with *Chrysanthemum leucanthemum*). The resemblance of *aragonensis* to these species in respect of its long antennal pubescence is clearly to be interpreted as convergence.

Phytomyza lindbergi Spencer

Phytomyza lindbergi Spencer, 1957 (p. 1—2) and 1965 a. Holotype ♂, La Palma (Canary Isles), in the University Zoological Museum, Helsinki.

Adult

Only a single strong lower orbital bristle *(ori)* present (2nd *ori* vestigial). Antennal pubescence short.

Six acrostichal hairs *(acr)* present.

Trochanters and the apex of the front coxae rather bright yellow.

♂ genitalia: Aedeagus (figs. 7 and 8) with the sclerites of the basiphallus becoming broad and obscurely defined towards their apex; distiphallus weakly developed; mesophallus slightly longer than in the other species of this group; the sac below the

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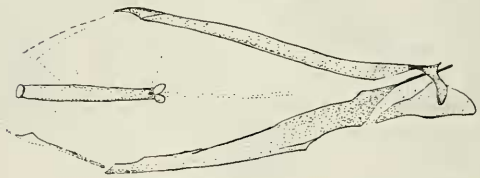

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Figs. 7—8. *Phytomyza lindbergi* Spencer holotype ♂: 7, aedeagus in lateral view; 8, aedeagus in ventral view. (Scale 0.1 mm.)

mesophallus is membranous and appears smaller than in the other species (the latter character however requires checking on fresh material). (Ejaculatory bulb lost.)

(♀ unknown.)

Material examined: Holotype ♂, El Paso (600 metres), La Palma, Canary Isles, 4. IV. 50, leg. Lindberg (HEL).

The holotype is still the only known specimen.

Spencer (1957) originally compared this species with *Phytomyza asteris* Hendel, but it is evident from the male genitalia that it should be included in the *syngenesiae* group. In *asteris* the aedeagus is of a somewhat different form, lacking the characteristic mesophallus of the *syngenesiae* group.

Phytomyza farfarella Hendel

Phytomyza farfarella Hendel, 1935 (p. 401). Holotype ♀, Jugoslavia, in the Naturhistorisches Museum, Vienna.

Phytomyza atricornis Meigen sensu Griffiths, 1964 and earlier records referring to Iceland (nomen dubium).

Adult

Usually only a single lower orbital bristle (*ori*) present, but a vestigial 2nd (lower) *ori* is found in a few specimens (including the holotype). Antennal pubescence short.

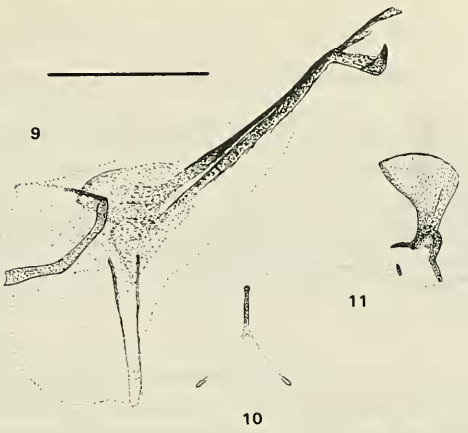
Usually 4—7 acrostichal hairs *(acr)* present, but no more than two in some Icelandic specimens.

Coxae and trochanters dark (contrast *lindbergi*). Basal cone of ovipositor (♀) grey dusted basally, but with about its apical third shining.

♂ genitalia: Aedeagus (figs. 9 and 10) with the sclerites of the basiphallus becoming broad and obscurely defined towards their apex; distiphallus weakly developed, sometimes hardly visible; mesophallus as in *syngenesiae*, with about its apical third bent upwards; the sac below the mesophallus is larger than in *syngenesiae* and more strongly sclerotised, especially along its hind margins. Ejaculatory bulb (fig. 11) usually with a rather longer "stalk" than in the other species of this group.

Material examined:

Yugoslavia — 2 ♀♀ (one the holotype), Bleder See, V., leg. Hendel (WIEN).



Figs. 9—11. *Phytomyza farfarella* Hendel ♂, Iceland: 9, aedeagus in lateral view; 10, distiphallus in dorsal view; 11, ejaculatory bulb. (Scale 0.1 mm.)

Germany — 1 ♂ ex *Taraxacum officinale* agg., Berlin-Finkenkrug, em. 3. VI. 24, leg. Hering no. 2447 (ISZ). 2 ♂♂ 1 ♀, same plant, Berlin-Frohnau, em. 24–27. VI. 25, leg. Hering (ISZ). 2 ♂♂, same plant and locality, em. 31. VII. 26, leg. Hering no. 2971 (ISZ). 1 ♂, same plant, Güntersberg an der Oder, em. 20. VI. 29, leg. Hering no. 1066 (ISZ).

Denmark — 1 ♀ ex *Leontodon autumnalis*, Lemvig, em. 5. VI. 50, leg. Sønderup (ISZ).

Sweden — 1 ♂ ex *Taraxacum* sp., Hedlandet, Södermanland, em. 30. VI. 43, leg. Lundqvist (LUND): 1 ♀, same host and locality, em 15. VII. 43, leg. Lundqvist (LUND).

Finland — 1 ♂, Saltvik, Åland, VII. 42, leg. Frey (HEL).

Ireland — 1 ♂, Lough Rask, near Ballyvaughan, Co. Clare, 3–8. VII. 60, leg. Coe (BM). 1 ♂ from the Haliday collection (NMI).

Faroes — 4 ♂♂, 2 ♀♀ from the islands of Streymoy, Nólsoy and Svinoy, as recorded in Griffiths, 1964 (KB).

Iceland — 44 ex. from localities in South and South-East Iceland, as recorded in Griffiths, 1964 (LUND and Göteborg Natural History Museum). 1 ♂, Skidastadalaug, Skagafjardarsýsla (North Iceland), 27. VII. 33, leg. Tuxen (KB). 4 ♂♂, Heimaey, Westmann Isles, 23. VII. 65 (2 ex.) and 13–14. VI. 66, leg. Andersson (LUND).

Other Fennoscandian localities given in the literature are Paanajärvi, near Kuusamo in northern Finland (Frey, 1946) and Gotland (Fridhem), Sweden (Rydén, 1952).

This is the only species of the *syngenesiae* group occurring in Iceland and the Faroes. I failed to distinguish it from *syngenesiae* and *horticola* when writing my work on the Agromyzid fauna of these islands (Griffiths, 1964), and consequently some of the comments on "*atricornis*" in that paper require revision. Since there is no evidence that *farfarella* is a species likely to be spread by human agency, I think it must be regarded as part of the indigenous fauna of these islands which is believed to have entered them during an interglacial period over a land-bridge from Europe. The species seems particularly common in the vicinity of hot springs in Iceland. My figure of the male genitalia of this species in that paper (Griffiths, 1964, fig. 4) was slightly misleading in one respect: the ejaculatory bulb figured is disproportionately large owing to a confusion in the scale of magnification. The ejaculatory bulb in this species is of similar relative size to that of other members of the *syngenesiae* group.

Phytomyza syngenesiae (Hardy)

Chromatomyia Syngenesiae Hardy, 1849 (p. 391), in part. Neotype ♂, Ireland, by present designation in the British Museum (Natural History): type locality, Scotland.

Phytomyza nigricornis M. Macquart sensu auctt. (e. g. Curtis, 1845) (nec *Phytomyza nigricornis* M. Macquart, 1835).

Phytomyza geniculata M. Macquart sensu auctt. (nomen dubium preoccupied by *Phytomyza geniculata* Brullé, 1832).

Phytomyza lateralis Fallén sensu auctt. (e. g. Goureau, 1851 and Robineau-Desvoidy, 1851) (nec *Phytomyza lateralis* Fallén, 1823).

Phytomyza albiceps Meigen sensu auctt. (e. g. Kaltenbach, 1874 [in part] and Watt, 1923) (nec *Phytomyza albiceps* Meigen, 1830).

Phytomyza affinis Fallén sensu auctt. (e. g. French, 1900) (nec *Phytomyza affinis* Fallén, 1823).

Phytomyza Chrysanthemi Kowarz in Lintner, 1891 (p. 242—243). Lectotpye ♂, U.S.A., by present designation in the Deutsches Entomologisches Institut, Eberswalde. **Syn. nov.**

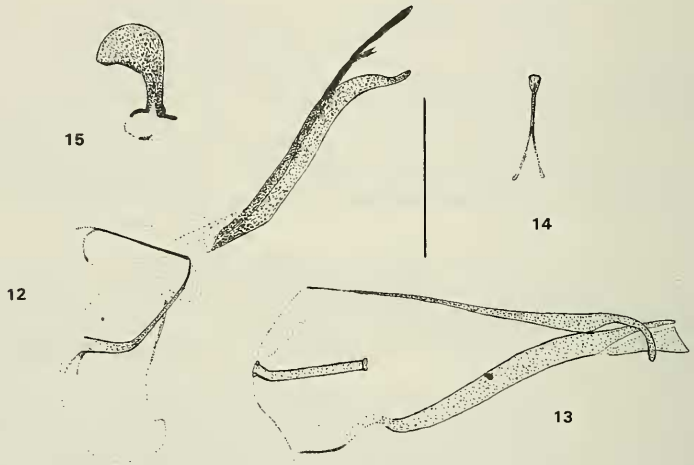
Phytomyza atricornis Meigen sensu Hendel, 1920 (in part) and widely in subsequent literature (nomen dubium).

Adult

Only a single lower orbital bristle (*ori*) present. Antennal pubescence short.

Acrostichal hairs (*acr*) often completely absent, at most one to four isolated hairs present. (Such specimens with a few *acr* present occur frequently in this species, but only rarely in *horticola*.)

Basal cone of ovipositor (♀) grey dusted basally, but with its apical half or third shining.



Figs. 12—15. *Phytomyza syngenesiae* (Hardy) ♂ ex *Chrysanthemum vulgare*, Ireland: 12, aedeagus in lateral view; 13, aedeagus in ventral view; 14, distiphallus in dorsal view; 15, ejaculatory bulb. (Scale 0.1 mm.)

♂ genitalia: Aedeagus (figs. 12—14) with the sclerites of the basiphallus becoming rather widely separated distally, more well defined towards their apex than in *farfarella* and *lindbergi;* distiphallus rather weakly developed, divergent only towards its apex; mesophallus with about its apical third bent upwards (as also in *farfarella*); the sac below the mesophallus is membranous (easily distorted in preserved specimens), rather smaller than in *farfarella*. Ejaculatory bulb (fig. 15) usually distinctly asymmetrical.

Material identified by examination of the aedeagus (♂♂ only)

Ireland — 1 ♂ neotype (by present designation) ex *Senecio jacobaea*, Doolin, Clare, em. 30. VIII. 66, leg. Griffiths (deposited in the British Museum [Natural History]). 1 ♂ ex *Senecio* sp., Dalkey, em. VI. 04 (NMI). 1 ♂ ex *Sonchus arvensis*, Poulsallagh, Clare, em. 20. VI. 65 (GCDG). 1 ♂ ex *Chrysanthemum leucanthemum*, Caherconnell, Clare, em. 26. VI. 65 (GCDG). 2 ♂♂ ex *Chrysanthemum vulgare*, Burren (near Ballyvaughan), Clare, em. 16 and 22. IX. 66 (GCDG).

Great Britain

Scotland — 1 ♂ ex *Chrysanthemum argyrophyllum*, Edinburgh, em. 15. VI. 53, leg. Spencer (KAS).

Wales — 1 ♂ ex *Inula crithmoides*, Burry Holms, Gower, em. 7. X. 62 (GCDG).

England — 1 ♂ ex *Senecio cruentus*, Bristol, em. IV. 20, leg. A. L. Smith (BM). 1 ♂ ex *Chrysanthemum* sp., Putney, London, em. VI. 18, leg. Cant (BM). 7 ♂♂ ex *Chrysanthemum* sp. (cultivated), Littlehampton, Sussex, leg. Hussey and Gurney (GCRI). 1 ♂ ex *Chrysanthemum* sp. (cultivated), Kensington, London, em. 1. VII. 15, leg. Robison (BM). 1 ♂ ex *Serratula tinctoria*, Woodside Park, London, em. 10. VIII. 53 (GCDG). 1 ♂ ex *Sonchus asper*, Whitby, Yorks., em. 15. VII. 37, leg. Britten (BM). 1 ♂ ex *Arnoseris minima* (labelled "*Lapsana pusilla*"), Middlesex, em. 3. VII. 23, leg. Heath (BM).

France — 1 ♂ ex *Anthemis* sp., Asnières, em. 7. IV. 1889, leg. Lesne (MNHN). 1 ♂ ex *Chrysanthemum leucanthemum*, 1899, leg. Blanchard (MNHN). 1 ♂ ex *Chrysanthemum* sp., Paris, em. 14.VII.46 (MNHN). 1 ♂ ex *Inula crithmoides*, La Baule, Loire inf., em. 15. IV. 43, leg. Buhr no. 4965 (ISZ).

Denmark — 1 ♂ ex *Daucus carota*, Copenhagen, em. 18. IX. 29, leg. Gudman (ISZ). 1 ♂ ex *Senecio squalidus*, Copenhagen Botanical Gardens, em. 15. XII. 65, leg. Sorensen (GCDG).

Sweden — 1 ♂ ex *Carduus crispus*, Hälsingborg, Skåne, em. 3. IX. 23, leg. Rydén (LUND). 1 ♂ ex *Taraxacum* sp., Hälsingborg, Skåne, em. 18. VII.23, leg. Rydén (LUND).

Finland — 1 ♂ ex *Chrysanthemum* sp., Hoplax, near Helsinki, 1936 (HEL).

Germany — 1 ♂ ex *Othonna integrifolia*, Berlin Botanical Gardens, em. 5. III. 34, leg. Hering (ISZ). 1 ♂ ex *Xeranthemum annuum*, Berlin, em. 28. VII. 24, leg. Hering no. 2584 (ISZ).

Yugoslavia — 1 ♂ ex *Sonchus oleraceus*, Lesina, Hvar Island, em. IV. 29, leg. Buhr (ISZ).

Spain — 1 ♂ ex *Sonchus oleraceus*, Irun, em. 10. IV. 33, leg. Hering no. 4101 (ISZ).

Canary Isles — 1 ♂ ex unidentified plant, Los Arucas, Gran Canaria, em. 21. II. 63, leg. Spencer (KAS). 1 ♂ (caught), Maspalomas, Gran Canaria, 9–10. III. 50, leg. Lindberg (HEL). 1 ♂ (caught), Pico de Teyde, Tenerife, 21–22. VII. 31, leg. Frey (HEL). 1 ♂ (caught), La Llanos, La Palma, 8. VIII. 31, leg. Storå (HEL).

Canada — 1 ♂ ex *Crepis* sp., Edmonton, Alberta, em. 4. VI. 66, leg. Sehgal (in Mr. Sehgal's collection). 1 ♂ ex *Senecio* sp., Frank, South Alberta (4,000 ft.), em. 1. VII. 66, leg. Spencer (KAS).

U.S.A. — 2 ♂♂ syntypes of *Phytomyza chrysanthemi* Kowarz (one of which is hereby designated lectotype), presumably Boston, Massachusetts (DEI): host-plant not stated, but presumably a cultivated *Chrysanthemum* species. 1 ♂ ex "daisy", Glendale, Rhode Island, em. 16. V. 10 (USNM). 1 ♂ ex "marguerite", Kingston, Rhode Island, em. 6. I. 16, leg. Stone (USNM). 1 ♂ ex lettuce (*Lactuca* sp.) in greenhouses, Puyallup, Pierce Co., Washington, em. 1. I. 53, leg. Frick (USNM). 1 ♂ ex *Sonchus* sp., Seattle, Washington, em. IV. 41 (USNM). 1 ♂ ex *Senecio cruentus*, San Francisco, California, em. 1. VI. 65, leg. Toschi & Tauber (BM). 1 ♂ ex *Dahlia* sp., San Francisco, California, leg. Whitney (USNM). 1 ♂ ex *Chrysanthemum* sp., Alameda Co., California, em. 21. IV. 11, leg. Aldrich (USNM). 1 ♂ ex *Zinnia elegans*, Albany, Alameda Co., em. 27. IX. 48, leg. Frick (USNM). 1 ♂ ex *Picris echioides*, Albany, Alameda Co., California, em. 3. VIII. 48, leg. Frick (USNM). 1 ♂ ex *Lactuca* sp., Albany, Alameda Co., California, em. 21. XI. 51, leg. Frick (USNM). 1 ♂ ex *Matricaria* sp., Berkeley, Alameda Co., California, em. 18. VI. 48, leg. Frick (USNM). 1 ♂ ex *Sonchus asper*, Berkeley, Alameda Co.,

California, em. 21. VII. 48, leg. Frick (USNM). 1 ♂ ex *Sonchus oleraceus,* Berkeley, Alameda Co., California, em. 1. VIII. 65, leg. Toschi and Tauber (KAS). 1 ♂ ex *Silybum marianum,* Berkeley, Alameda Co., California, em. 23. XII. 48, leg. Frick (USNM). 1 ♂ ex *Pisum sativum,* Berkeley, Alameda Co., California, em. 14. VII. 17, leg. Aldrich (USNM). 1 ♂ ex *Cynara scolymus,* Half Moon Bay, California, em. 11. V. 37, leg. Lange (USNM). 1 ♂ ex *Helianthus californicus,* ? California, leg. Whitney (USNM).

Australia — 1 ♂ ex *Senecio jacobaea,* Leongatha, Victoria, em. 16. VII. 27, leg. Hill (CSIRO). 2 ♂♂ (caught), same locality, undated and 31. VIII. 27, leg. Hill (CSIRO). 1 ♂ (caught), Bronte, New South Wales, 8. IX. 54, leg. McAlpine (AM). 1 ♂ (caught), Belltrees, near Scone, New South Wales, 19. X. 56, leg. McAlpine (AM). 1 ♂ (caught), North Beach, Bellinger River, New South Wales, 16. XI. 64, leg. McAlpine (AM). 1 ♂ (caught), Sydney University, New South Wales, 23. IX. 54, leg. McAlpine (AM).

New Zealand — 2 ♂♂ ex *Sonchus* sp., Canterbury, em. 11. VII. 63, leg. Yoong (GCDG).

The absence of records of this species from the Eastern part of the Palaearctic region hardly seems significant in view of the limited material of the *syngenesiae* group available to me from that area. I think it probable that *syngenesiae* is a holarctic species which has been able to spread across the former land connection between Siberia and Alaska. Its extensive distribution in North America suggests that it is not a recent introduction there.

I have no doubt that the occurrence of this species in Australia and New Zealand is the result of recent introduction. There seems no significant morphological differentiation in the material I have seen from these countries, and the recorded host range there includes many introduced plants.

It is evident from the records given above that this species usually develops in Compositae hosts. The range of Compositae attacked is clearly very wide, although there are no records for a few genera (e.g. *Aster* and *Solidago*). Whether these apparent gaps are fortuitous or represent real discontinuities in the host range is not yet clear.

The occurrence of this species on hosts other than Compositae appears to be rare, and may be regarded as xenophagy. Details of one North American specimen labelled as bred from *Pisum* (Leguminosae) have been given above, and Frick (1959) also records *Mentha* sp. and *Stachys bullata* (Labiatae), *Malva borealis* (Malvaceae) and *Melilotus indica* (Leguminosae) as hosts of "*Phytomyza atricornis* Meigen" in North America. It seems probable that some or all of these records refer to *syngenesiae* (since *horticola* is not known in North America), but confirmation from the dissection of males bred from these hosts seems desirable before they can be finally accepted. From Australia I have received one female presumably referable to this species which was bred from *Urtica incisa* (Urticaceae) (Jenolan Caves, 2,000 ft., New South Wales, leg. Wiburo [AM]), and Hendel (1934) also recorded a specimen of "*atricornis*" bred from *Urtica ferox* in New Zealand. Watt's (1923) and Harrison's (1959) lists of hosts of "*atricornis*" in New Zealand also include *Plantago* spp. (Plantaginaceae) and *Melilotus* sp. (Leguminosae). However the former record requires careful checking in view of the possibility of confusion with *Phytomyza plantaginis* Robineau-Desvoidy; and the latter record was clearly doubtful, as Watt prefixed it with the word "possibly". From Europe I have discovered only one case of *syngenesiae* having been bred from a non-Compositae host, the record for *Daucus* (Umbelliferae) given above. But it would be unwise to assume from this evidence that the host tolerance of European strains of *syngenesiae* is less than that shown in other parts of the species' range. The abundance of *horticola* on non-Compositae hosts must inevitably tend to mask the rarer occurrence of *syngenesiae* on such hosts in areas where both species occur. Any apparent diffe-

rence in host tolerance in the Palaearctic region should therefore be regarded with caution unless confirmed by laboratory experiments.

Complete lists of the host records which seem attributable to this species (subject to the remarks above) in areas where no other species of the *syngenesiae* group occurs have been given by SPENCER (1963) for Australia, HARRISON (1959) for New Zealand and FRICK (1959) for North America. One correction of FRICK's list should however be noted. The series which he bred from *Gnaphalium leucocephalum* in California does not represent a species of the *syngenesiae* group, but a species related to the European *Phytomyza ciliata* Hendel and *P. farfarae* Hendel.

Phytomyza horticola Goureau

Phytomyza horticola Goureau, 1851 (p. 148—149). Neotype ♂, Germany, by present designation in the Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität, Berlin: type locality, France.

Phytomyza geniculata M. Macquart sensu auctt. (e. g. ROBINEAU-DESVOIDY, 1851 and GOUREAU, 1861 and 1869) (nomen dubium preoccupied by *Phytomyza geniculata* Brullé, 1832).

Phytomyza cucumidis J. Macquart, 1854 (p. 235) (nomen nudum). **Syn. nov.**

Phytomyza Tropaeoli Dufour, 1857 (p. 45). Types lost: type locality, France. **Syn. nov.**

Phytomyza Fediae Kaltenbach, 1860 (p. 250). Types lost: type locality, Germany. **Syn. nov.**

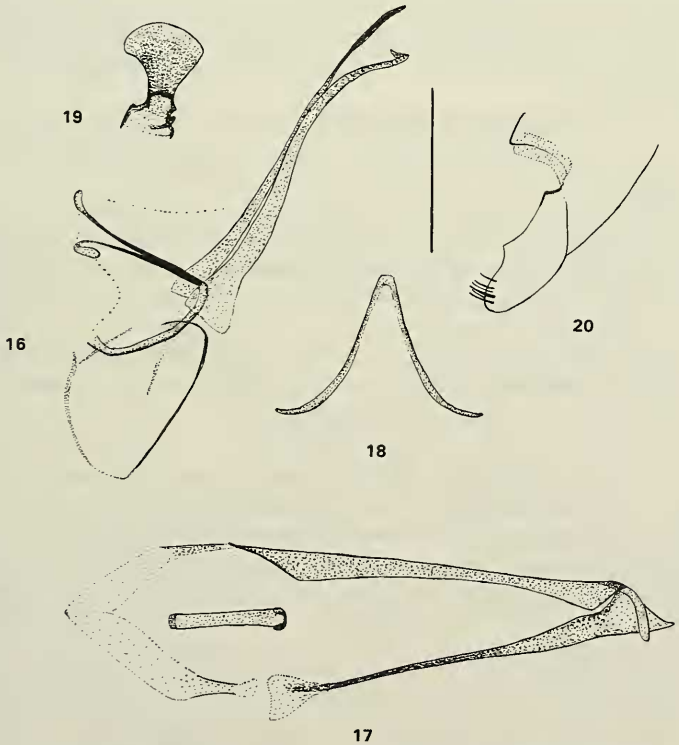
Phytomyza Linariae Kaltenbach, 1862 (p. 83) and 1874. Types lost: type locality, Germany. **Syn. nov.**

Phytomyza Pisi Kaltenbach, 1864 (p. 305) and 1874. Types lost: type locality, Germany. **Syn. nov.**

Phytomyza albiceps Meigen sensu auctt. (e. g. KALTENBACH, 1874, in part) (nec *Phytomyza albiceps* Meigen, 1830).

Phytomyza subaffinis Malloch, 1914 (p. 335). Holotype ♀, Formosa, in the Hungarian Natural History Museum, Budapest. **Syn. nov.**

Phytomyza atricornis Meigen sensu Hendel, 1920 (in part) and widely in subsequent literature (nomen dubium).



Figs. 16—20. *Phytomyza horticola* Goureau ♂ ex *Linaria*, Italy: 16, aedeagus in lateral view; 17, aedeagus in ventral view; 18, distiphallus in dorsal view; 19, ejaculatory bulb; 20, surstylus and part of 9th tergite (epandrium) in posteroventral view. (Scale 0.1 mm.)

Napomyza lactucae Vimmer, 1926 (p. 117). Syntype ♀, Czechoslovakia, in Mr. K. A. Spencer's collection, London. **Syn. nov.**

Phytomyza bidensivora Séguy, 1951 (p. 313—314), Paulian, 1953 and Spencer, 1959. Lectotype ♂, Madagascar, by present designation in the Muséum National d'Histoire Naturelle, Paris. **Syn. nov.**

Adult

Only a single lower orbital bristle (*ori*) present. Antennal pubescence short.

Acrostichal hairs (*acr*) usually completely absent, rarely one or two isolated hairs present.

Basal cone of ovipositor (♀)grey dusted basally, but with its apical half or third shining.

♂ genitalia[1]: Aedeagus (figs. 16—18) with the distiphallus strongly developed, divergent from its base; mesophallus more evenly curved than in *syngenesiae* and *farfarella*, bent upwards only at its apex; the sides of the sac below the mesophallus form a pair of sclerotised plates which unite apically (fig. 17); these are largely transparent but with a variable degree of pigmentation along their margins. Ejaculatory bulb (fig. 19) usually almost symmetrical, rarely as strongly asymmetrical as that figured for *syngenesiae* (compare fig. 15).

Material identified by examination of the aedeagus (♂♂ only)

Ireland — 1 ♂ ex *Pisum sativum*, from the Haliday collection (NMI).

England — 1 ♂ ex *Vicia sepium*, Faversham, Kent, em. 7. VII. 54 (GCDG). 2 ♂♂ ex *Dahlia* sp., Littlehampton, Sussex, leg. Hussey & Gurney (GCRI). 1 ♂ ex *Allium sativum* in my garden at Barnet, London, em. 24. VI. 66 (GCDG).

France — 1 ♂ ex *Lepidium draba*, Hyères, em. 21. V. 35, leg. Wilson (BM). 1 ♂ ex *Lycium* sp., em. VII. 26, leg. Lesne (MNHN). 1 ♂ ex *Senecio vulgaris*, Tence (H. L.), em. 8. VII. 27, leg. Meneval (MNHN). 1 ♂ ex *Arctium lappa*, Paris, em. 28. VI. 53, leg. Spencer (KAS). 1 ♂ ex *Cirsium vulgare*, La Baule, Loire inf., em. 5. VI. 43, leg. Buhr no. 386 (ISZ). 1 ♂ ex *Allium cepa*, Cherbourg, em. 10. VI. 28, leg. Hering (ISZ).

Switzerland — 1 ♂ ex *Inula hirta*, Lenzerheide, em. 16. VII. 25, leg. Hopp (ISZ).

Denmark — 1 ♂ ex *Taraxacum officinale* agg., Lemvig, Denmark, em. 10. X. 53, leg. Sønderup (KAS).

Sweden — 1 ♂ ex *Brassica campestris* var. *capitata*, Hälsingborg, Skåne, em. 19. VIII. 23, leg. Rydén (LUND). 1 ♂ ex *Linum usitatissimum*, Hälsingborg, Skåne, em. 2. IX. 24, leg. Rydén (ISZ). 1 ♂ ex *Pisum sativum*, Hedlandet, Södermanland, em. 23. VII. 43, leg. Lundqvist (LUND). 1 ♂ ex *Melilotus albus*, Hälsingborg, Skåne, em. 2. VIII. 27, leg. Rydén (LUND). 1 ♂ ex *Matricaria* sp., Sønderup, em. 17. VII. 52, leg. Rydén (LUND). 1 ♂ ex *Senecio vulgaris*, Hälsingborg, Skåne, em. 30. VI. 23, leg. Rydén (LUND). 1 ♂ ex *Helichrysum* sp., Hedlandet, Södermanland, em. 22. VIII. 43, leg. Lundqvist (LUND).

Finland — 1 ♂ (caught), Forvas, leg. Frey (HEL).

Germany — 1 ♂ ex *Adonis aestivalis*, Erfurt, Schwellenburg, Thuringia, em. 12. VI. 58, leg. Buhr no. 1352 (KAS). 1 ♂ ex *Brassica napus*, Kiel, em. IX. 28, leg. Blunck (ISZ). 1 ♂ ex *Conringia orientalis*, Rostock Botanical Gardens, Mecklenburg, em. 5. VII. 49, leg. Buhr no. 182 (ISZ). 1 ♂ ex *Thlaspi arvense*, Masserberg, Thuringia, em. 11. X. 58, leg. Buhr no. 1449 (ISZ). 1 ♂ ex *Papaver* sp., Jerichow (Elbe), em. 8. VII. 23, leg. Hering no. 2305 (ISZ). 1 ♂ ex *Papaver* sp., Aschersleben, leg. Nolte, VI. 50 (DEI). 1 ♂ ex *Cleome dodecandra*, Rostock, Mecklenburg, em. 27. VII. 32, leg. Buhr (ISZ). 1 ♂ neotype (by present designation) ex *Tropaeolum majus*, Jerichow (Elbe), em. 23. VII. 22, leg. Hering no. 2085 (ISZ). 1 ♂ ex *Cerastium semidecandrum*, Berlin-Frohnau, em. 13. VI. 26, leg.

[1] The description relates to typical material from the Palaearctic and Oriental Regions. Geographical variation in the Ethiopian Region is discussed below.

Hering (ISZ). 1 ♂ ex *Salicornia herbacea*, Rostock Botanical Gardens, Mecklenburg, em. 12. VIII. 37, leg. Buhr (ISZ). 1 ♂ ex *Ononis hircina*, Rostock, Mecklenburg, em. 26. VI. 35, leg. Buhr (ISZ). 1 ♂ ex *Pisum sativum*, Aschersleben, leg. Nolte, VI. 50 (DEI). 1 ♂ ex *Pimpinella anisum*, Rostock Botanical Gardens, Mecklenburg, em. 12. VII. 36, leg. Buhr (ISZ). 1 ♂ ex *Tordylium persicum*, Mecklenburg, em. 21. VI. 37, leg. Buhr (ISZ). 1 ♂ ex *Asperugo procumbens*, Schwäbischer Jura, em. 12. VIII. 23, leg. Hering no. 2369 (ISZ). 1 ♂ ex *Lithospermum officinale*, Bellinchen Mark, em. 4. VI. 26, leg. Hering no. 2887 (ISZ). 1 ♂ ex *Symphytum officinale*, Kirschberge, Mühlhausen, Thuringia, em. 7. VI. 66, leg. Buhr no. 2800 (GCDG). 1 ♂ ex *Echium vulgare*, Bredow bei Nauen, em. 29. VII. 23, leg. Hering no. 2337 (ISZ). 1 ♂ ex *Satureia hortensis*, Berlin-Frohnau, em. 3. IX. 26, leg. Hering no. 2952 (ISZ). 1 ♂ ex *Phlox drummondi*, Rostock, Mecklenburg, em. 3. VIII. 35, leg. Buhr no. 77/7 (ISZ). 1 ♂ ex *Linaria vulgaris*, Jerichow (Elbe), em. 9. VII. 23, leg. Hering no. 2303 (ISZ). 1 ♂ ex *Valeriana sambucifolia*, Rostock, Mecklenburg, em. 6. VI. 35, leg. Buhr no. 682 a (ISZ). 1 ♂ ex *Valeriana officinalis*, Jerichow (Elbe), em. 5. VII. 23, leg. Hering no. 2302 (ISZ). 1 ♂ ex *Centaurea jacea*, Berlin-Dahlem, em. 27. VI. 42, leg. Hering no. 4838 (ISZ). 1 ♂ ex *Doronicum austriacum*, Berlin Botanical Gardens, em. 24. VI. 23, leg. Hering no. 2235 (ISZ). 1 ♂ ex *Chrysanthemum corymbosum*, Berlin Botanical Gardens, em. 28. VI. 23, leg. Hering no. 2241 (ISZ). 1 ♂ ex *Chrysanthemum vulgare*, Berlin-Frohnau, em. 6. VII. 26, leg. Hering no. 2946 (ISZ). 1 ♂ ex *Artemisia dracunculus*, Berlin-Frohnau, em. 13. VII. 26, leg. Hering no. 2959 (ISZ). 1 ♂ ex *Senecio vernalis*, Berlin, em. VI. 26, leg. Hopp (ISZ). 1 ♂ ex *Senecio vulgaris*, Berlin-Dahlem, em. 12. VI. 48, leg. Hering no. 5420 a (ISZ). 1 ♂ ex *Erigeron canadense*, Berlin-Frohnau, em. 8. VI. 26, leg. Hering no. 2921 (ISZ). 1 ♂ ex *Anthemis tinctoria*, Stempeda, Harz, em. 25. VI. 27, leg. Hering no. 3158 (ISZ). 1 ♂ ex *Taraxacum officinale* agg., Berlin-Frohnau, em. 1. VIII. 26, leg. Hering no. 2971 (ISZ).

Austria — 1 ♂ ex *Centaurea jacea*, Linz, Upper Austria, em. 1. VII. 62, leg. Hering no. 6792 (KAS).

Poland — 1 ♂ ex *Hesperis matronalis*, Rabendorf, Silesia, leg. Teichel (ISZ).

Russia — 1 ♂ ex *Brassica juncea*, Rostov-on-Don, em. 17. VI. 27, leg. Mamonow (ISZ). 1 ♂ ex *Ononis hircina*, Rostov-on-Don, em. 12. VII. 27, leg. Mamonow (ISZ). 1 ♂ ex *Cicer arietinum*, Rostov-on-Don, em. 7. VII. 27, leg. Mamonow (ISZ). 1 ♂ ex *Vigna sinensis*, Rostov-on-Don, em. 28. VI. 27, leg. Mamonow (ISZ).

Yugoslavia — 1 ♂ ex *Chrysanthemum coronarium*, Jelsa, Hvar Island, em. 12. V. 65, leg. Hering no. 7326 (ISZ). 1 ♂ ex *Cirsium creticum*, Jelsa, Hvar Island, em. 27. V. 65, leg. Hering no. 7399 (ISZ).

Italy — 3 ♂♂ ex *Linaria* sp., Ostia, near Rome, em. 18. IV. 54 (GCDG). 1 ♂ ex *Senecio doria*, Rome, em. 7. I. 65, leg. Frick (KAS).

Corsica — 1 ♂ ex *Isatis* sp., Corté, em. IX. 33, leg. Buhr (ISZ).

Sicily — 1 ♂ (caught), Sinofsi, Mount Etna, 8. IV. 64, leg. Spencer (KAS).

Spain — 2 ♂♂ ex *Sisymbrium orientale*, Albarracin, Aragon, em. VI. 33, leg. Hering no. 4222 (KAS and ISZ). 3 ♂♂ (caught), Mongat, near Barcelona, 21. II. 10, coll. Lichtwardt (DEI).

Portugal — 1 ♂ ex *Gazania* sp., Lisbon, em. 4. IV. 53, leg. Spencer (KAS).

Azores — S. Miguel. 1 ♂, Ponta Delgada, 12. V. 38, leg. Storå (HEL). 1 ♂, Furnas, 19–21. V. 38, leg. Storå (HEL).
Terceira. 1 ♂, Santa Barbara, 7. VI. 38, leg. Frey (HEL). 1 ♂, Achada, 3–4. VI. 38, leg. Frey (HEL).
Pico. 1 ♂, Madalena, 6–9. VII. 38, leg. Storå (HEL).

Fayal. 3 ♂♂, Caldeira, 4. VII. 38, leg. Frey (HEL).
Flores. 1 ♂, Santa Cruz, VI. 38, leg. Storå (HEL). 1 ♂, Ribeira Fazenda, VI. 38, leg. Storå (HEL).
Corvo. 1 ♂, Caldeiras, 24. VI. 38, leg. Storå (HEL).

Madeira — 1 ♂, Funchal, 1–8. V. 38, leg. Frey (HEL). 1 ♂, Porto Novo, 5. V. 38, leg. Frey (HEL).

Canary Isles — 2 ♂♂ ex *Malva neglecta*, Santa Cruz, Tenerife, em. 16–17. III. 26, leg. Hering no. 2765 (ISZ). 2 ♂♂ ex *Lathyrus tuberosus*, Laguna, Tenerife, em. 14–15. III. 26, leg. Hering no. 2778 (KAS and ISZ). 1 ♂ ex *Plantago lanceolata*, Puerto de Cabras, Fuerteventura, em. 21. III. 26, leg. Hering no. 2784 (ISZ). 1 ♂ ex *Bystropogon plumosum*, El Paso, Palma, em. 11. IV. 26, leg. Hering no. 2830 (ISZ). 1 ♂ ex *Lithospermum arvense*, Puerto de Cabras, Fuerteventura, em. 27. III. 26, leg. Hering no. 2788 (ISZ). 1 ♂ ex *Bidens pilosus*, Santa Cruz, La Palma, em. 16. IV. 26, leg Hering no. 2808 (ISZ). 1 ♂ ex *Carduus baeocephalus*, Laguna, Tenerife, em. 28. IV. 26, leg. Hering no. 2875 (ISZ). 2 ♂♂ (caught), Las Palmas, Gran Canaria, 28–30. VI. 31, leg. Frey and Storå (HEL). 1 ♂ (caught), Chilegua, Fuerteventura, 4–14. III. 49, leg. Lindberg (HEL). 2 ♂♂ (caught), Haria, Lanzarote, 19. III. 49, leg. Lindberg (HEL).

Morocco — 1 ♂ ex Compositae sp., Casablanca, em. 28. I. 66, leg. Spencer (KAS).

Egypt — 1 ♂ ex *Pisum sativum*, Heliopolis, em. 20. XII. 21, leg. Hargreaves (BM). 1 ♂ ex *Solanum melongena*, Alexandria, em. 29. III. 56, leg. Hammad (ISZ).

Palestine — 1 ♂ ex *Eruca sativa*, Tel Aviv, leg. Bodenheimer (ISZ). 1 ♂ ex *Papaver somniferum*, Tel Aviv, leg. Bodenheimer (ISZ). 1 ♂ ex *Pisum sativum*, Tel Aviv, leg. Bodenheimer (ISZ). 1 ♂ ex *Linaria vulgaris*, Tel Aviv, em. 21–30. IV. 26, leg. Bodenheimer (ISZ). 1 ♂ ex *Chrysanthemum* sp., Tel Aviv, leg. Bodenheimer (ISZ). 1 ♂ ex *Sonchus oleraceus*, Tel Aviv, em. II. 26, leg. Bodenheimer (ISZ).

India — 1 ♂ ex *Melilotus parviflora*, Lyallpur, Punjab, em. 19. II. 23, leg. Bahadur (BM). 1 ♂ ex *Pisum sativum*, Lyallpur, Punjab, em. 19. III. 20, leg. Bahadur (BM). 1 ♂ ex *Chrysanthemum* sp., Lyallpur, Punjab, em. 16. III. 23, leg. Bahadur (BM). 1 ♂ ex *Sonchus asper*, Lyallpur, Punjab, em. 23. III. 20, leg. Bahadur (BM).

China — 1 ♂ ex *Brassica* f. *oleifera*, Shanghai, em. V. 33, leg. Hoene (ISZ). 1 ♂ ex *Papaver somniferum*, Shanghai, em. V. 33, leg. Hoene (ISZ). 1 ♂ ex *Pisum sativum*, Canton, leg. Hoffman (BM). 1 ♂ ex *Linum usitatissimum*, Canton, leg. Hoffman (BM). 2 ♂♂ ex *Carduus* sp., Charbin, Manchuria, em. 5–10. VI. 51, leg. Alin (ISZ). 1 ♂ ex *Helianthus annuus*, Charbin, Manchuria, em. 8. V. 51, leg. Alin (ISZ).

Formosa — 1 ♂ (paratype of *Phytomyza subaffinis* Malloch), Tainan, II. 1909, leg. Sauter (Hungarian Natural History Museum). 1 ♂ ex *Solanum indicum*, Taipei, em. 7. IV. 65, leg. Sasakawa (GCDG).

Japan — 1 ♂ ex *Artemisia vulgaris*, Ashoro, Hokkaido, em. 16. IV. 54, leg. Sasakawa (GCDG). 1 ♂ ex *Nasturtium indicum*, Kibune (Yamashiro), Honshû, em. 19. V. 53, leg. Sasakawa (GCDG). 1 ♂ ex *Chrysanthemum* sp., Kibune (Yamashiro), Honshû, em. 7. V. 53, leg. Sasakawa (GCDG). 1 ♂ ex *Mentha arvensis*, Hikosan (Buzen), Kyûshû, em. 24. V. 56, leg. Sasakawa (GCDG).

Cape Verde Isles — 1 ♂ (caught), S. Antão Cova, 31. XII. 53, leg. Lindberg (HEL).

Cameroons — 1 ♂ ex *Veronica* sp., Cameroon mountain (2,900 metres), em. 17. V. 38, leg. Buhr (ISZ).

Eritrea — 1 ♂ ex *Brassica oleracea*, Actia (2,350 metres), Asmara, em. 22. XII. 46, leg. de Lotto (BM).

Kenya — 1 ♂ ex *Petunia* sp., em. 12. VIII. 40, leg. Pelley (BM). 1 ♂ ex *Galinsoga parviflora*, Nairobi, em. 1. XII. 61, leg. Spencer (KAS).

Madagascar — 1 ♂ (lectotype by present designation of *Phytomyza bidensivora* Séguy) ex *Bidens pilosa*, Tsimbazaza, near Tananarive, em. 15. IV. 49 (MNHN).

South Africa — 1 ♂ ex *Solanum nigrum*, Stellenbosch, em. 8. XII. 61, leg. Spencer (KAS).

Distribution and Geographical Variation

The above records indicate that this species is very widely distributed throughout the Old World from highboreal to subtropical areas, but it seems entirely absent from the New World. The most northerly record is that for Finland. The species is evidently very common both in temperate areas, such as central Europe, and in warmer areas such as China, Japan, India and the Mediterranean. But the available records for tropical latitudes all refer to localities at substantial altitudes. It is not yet clear whether the species can exist at sea level on the equator.

Other records in the literature which most probably refer to *horticola*, for countries other than those listed above, are as follows.

Indonesia — Kalshoven (1951) gives an account of "*atricornis*" attacking *Pisum sativum* in western Java.

Thailand — 1 ♀, Chiangmai, Suthep (1,278 m) recorded by Spencer (1962).

Libya — Damiano (1962) records "*atricornis*" as a pest of "fava" (presumably *Vicia faba*) in Tripolitania.

Senegal — Risbec (1950) records "*atricornis*" as occurring on *Lactuca*.

Abyssinia — Spencer (1964) reported females of "*atricornis*" bred from *Mikaniopsis* and *Cotula*.

Congo (Leopoldville) — Spencer (1959) reported "isolated records".

In all the above countries the occurrence of any species of the *syngenesiae* group except *horticola* seems unlikely.

In the lectotype of *bidensivora* (from Madagascar) and the males examined from South Africa, Kenya, Eritrea and the Cameroons, the sac below the mesophallus is slightly larger than in material from other areas, with its hind margin forming a more pronounced angle with the basiphallus (fig. 21). It is possible that an analysis of more numerous material from the Ethiopian region will enable the definition of a geographical subspecies (for which the name *bidensivora* is available) on the basis of this variation. But I am not able to offer a firm opinion on this question at present, since only six males have been available to me from these areas. The single male from the Cape Verde Isles agrees well with material from Europe and the other Atlantic islands.

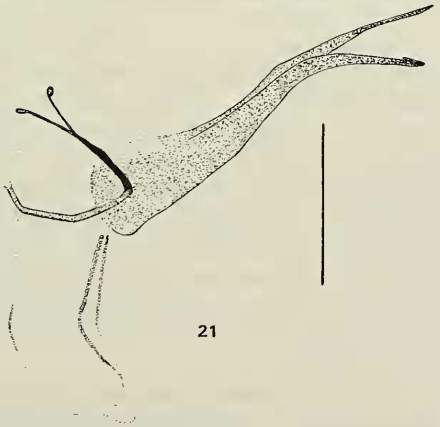


Fig. 21. *Phytomyza horticola* Goureau ♂ (lectotype of *P. bidensivora* Séguy), aedeagus in lateral view. (Scale 0.1 mm.)

I have noticed no obvious geographical variation in this species outside the Ethiopian Region.

It is clear from the account of „*Phytomyza atricornis* Meigen" in Hering (1957 b) that this species normally produces a linear mine in Africa, as elsewhere. Some confusion has arisen because the figure in Paulian (1953) of the mines from which Séguy's original material of *bidensivora* was bred appears to portray virtual blotch mines. However Paulian's verbal description ("circonvolutions larges, superficielles, très serrées et parfois contigués . . .") clearly does not refer to true blotch mines, but to convolute linear mines which tend to form a secondary blotch. I do not think that any great significance can be attached to this discrepancy between Hering's and Paulian's account of the mine: the most likely explanation is that Paulian has figured somewhat untypical examples.

Host Range

This species is one of the few polyphagous species of Agromyzidae, having a host range matched only by a few American *Liriomyza* spp. The recorded hosts include one monocotyledonous genus, *Allium*, as well as a very large number of dicotyledons. But the range is by no means continuous. Many large groups of plants (e. g. the Rosaceae and Amentiferae) are avoided entirely, and others (e. g. the Ranunculaceae and Caryophyllaceae) appear to be only very rarely attacked. The fairly extensive information now available on hosts in Europe, India and Japan suggests that the host range is substantially the same throughout the Palaearctic and Oriental regions. The information for the Ethiopian region (where some slight morphological variation is apparent, as discussed above) is still rather meagre, but suggests that the host range there too is similar to that in the other regions.

I have attempted to summarise the confirmed and probable host genera of this species in the table below. The confirmed host records (indicated in bold type) are based solely on the list of identified males given above. The basis of my acceptance of the other recorded host genera of "*atricornis*" as probable hosts of *horticola* is as follows:

Europe — Only confirmed records for Compositae hosts are included in the table, since there is no basis for attributing other records of "*atricornis*" to this species rather than *syngenesiae*. Most of the probable records for non-Compositae hosts result from or have been confirmed by the work of Buhr, Hering and de Meijere: a long list of hosts in Czechoslovakia was also given by Starý (1930). References are given to the sources of the few records not confirmed by these workers, or added since the publication of Hering's (1957 a) most recent keys to European leaf-miners. The few records of „*atricornis*" referring to Dipsacaceae are however omitted, since I suspect they may be based on confusion with species not belonging to the *syngenesiae* group. The single record for *Avena* (Gramineae) (de Meijere, 1926) is also omitted. De Meijere's figure of the genitalia of this specimen, although not sufficiently detailed for a firm identification, probably refers to *horticola*. But a confusion in the data must be suspected in the absence of any confirmation of the occurrence of this species on Gramineae hosts.

North Africa and Palestine — My sources of additional records are Amsel and Hering (1931), Kozlowsky and Rungs (1932), Hammad (1955), Damiano (1962) and Rivnay (1962). No other species of the *syngenesiae* group is known from this area.

Canary Isles — Only confirmed records for Compositae hosts are included in the table, since *syngenesiae* also occurs on these islands. Other records for non-Compositae hosts are derived from Hering (1927).

India — My sources of additional records are Ahmad and Gupta (1941), Trehan and Sehgal (1963) and Sehgal (1965). No other species of the *syngenesiae* group is known from this area.

China — Additional records for Northern China are based on Sasakawa (1956).

Japan — Although I have only been able to confirm the occurrence of *horticola* in Japan, it seems unwise to assume that *syngenesiae* is absent on the basis of the limited material available to me: I have therefore only included the confirmed records of *horticola* from Compositae hosts in the table. The additional records for non-Compositae hosts are derived from the list given by Sasakawa (1961b).

Java — The single record is based on Kalshoven (1951).

Ethiopian Region — The sources of additional records are de Lotto (1948), Risbec (1950), Hering (1957b) and Spencer (1959 and 1964). No other species of the *syngenesiae* group is known from this region.

Table:

Summary of Host Range of *Phytomyza horticola* Goureau

Abbreviations:

A a	Ethiopian Region (Africa south of the Sahara)
C	Southern China (Shanghai, Formosa and Canton)
E e	Europe (including the British Isles)
I i	India
J j	Japan
jv	Java
K k	Canary Isles
M m	Northern China (Palaearctic region)
N n	North Africa and Palestine

The names of host genera confirmed by the examination of the genitalia of males bred from them are printed in **bold roman type**, and the area to which such confirmed records relate indicated by the use of a **bold capital** letter for the appropriate abbreviation.

Monocotyledones

Liliaceae

Allium, E i j.

Dicotyledones

Cannabaceae

Cannabis, e i j; *Humulus,* e.

Polygonaceae

Polygonum, e j.

Chenopodiaceae

Chenopodium, a e (Voigt, 1929) j; *Spinacia,* i; *Atriplex,* e; **Salicornia, E.**

Amaranthaceae

Amaranthus, e.

Caryophyllaceae

Gypsophila, e (Séguy, 1934); *Stellaria,* e; **Cerastium, E.**

Ranunculaceae

Adonis, E.

Papaveraceae

Papaver, C E i **N**; *Glaucium,* e.

Capparaceae

Cleome, E.

Cruciferae

Heliophila, e; **Brassica, A C E** i j m n; *Erucastrum,* e; *Hirschfeldia,* e; *Brassicella,* e; **Eruca,** e i **N**; *Sinapis,* e; *Diplotaxis,* e; *Raphanus,* e i j m; *Calepina,* e; *Crambe,* e; *Cakile,* e; **Conringia, E; Lepidium** (incl. *Cardaria*), **E** i;

Coronopus (= *Senebiera*), e i; **Isatis**, E; *Iberis*, e; *Biscutella*, e; **Thlaspi**, **E**; *Capsella*, e; *Cochlearia*, e; *Myagrum*, e; *Bunias*, e; *Peltaria*, e; *Berteroa*, e; *Cardamine*, e j; *Barbarea*, e; *Arabis*, e; *Turritis*, e; **Rorippa** (incl. *Nasturtium*), a e **J**; *Moricandia*, e; *Matthiola*, e; **Hesperis**, **E**; *Erysimum*, e; *Cheiranthus*, a e i; *Alliaria*, e; **Sisymbrium**, **E** i; *Arabidopsis*, e; *Descurainia*, e.

Resedaceae

Reseda, e.

Leguminosae

Lupinus, e i n; **Ononis**, **E**; *Trigonella*, e i; **Melilotus**, **E I** n; *Medicago*, a e j m n; *Trifolium*, e i j n; *Anthyllis*, e; *Tetragonolobus*, e; *Tephrosia*, i; *Phaca*, e; *Galega*, e; *Oxytropis*, e; *Scorpiurus*, e; **Cicer**, **E**; *Lens*, e i; **Vicia**, **E** j n; **Lathyrus**, a e i j **K**; **Pisum**, a **C E I** j j^{v} m **N**; *Glycine*, e; *Phaseolus*, e; *Dolichos*, e; **Vigna**, **E**; *Amphicarpaea*, e.

Buhr (1953) gives an analysis of the frequency of "*atricornis*" on different genera of Leguminosae in Germany.

Tropaeolaceae

Tropaeolum, **E** i j.

Linaceae

Linum, **C E** i j.

Rutaceae

Ruta, e.

Euphorbiaceae

Euphorbia, e.

Anacardiaceae

Rhus, e; *Cotinus*, e.

Malvaceae

Althaea, e i; *Lavatera*, e; **Malva**, e i j **K**; *Anoda*, e; *Palava*, e; *Hibiscus*, e j; *Kitaibelia*, e.

Violaceae

Viola, i.

Onagraceae

Oenothera, e.

Umbelliferae

Eryngium, e; *Coriandrum*, e; *Conium*, e; *Apium*, e; *Petroselinum*, e; **Pimpinella**, **E**; *Seseli* (incl. *Libanotis*), e; *Anethum*, e; *Levisticum*, e; *Ferula*, e; *Peucedanum*, e; **Tordylium**, **E**; *Daucus*, i.

Convolvulaceae

Convolvulus, e.

Polemoniaceae

Phlox, **E** i j n; *Polemonium*, e.

Hydrophyllaceae

Phacelia, e; *Nemophila*, e.

Boraginaceae

Heliotropium, e; *Cynoglossum*, e; *Omphalodes*, e; *Trichodesma*, e; *Caccinia*, e; *Lappula*, e; **Asperugo**, **E**; *Anchusa*, e; *Lycopsis*, e; *Nonea*, e; *Pulmonaria*, e; **Symphytum**, **E**; *Borago*, e; **Lithospermum**, **E K**; *Myosotis*, e; *Cerinthe*, e; *Podonosma*, n; **Echium**, **E**.

Verbenaceae

Verbena, e.

Labiatae

Ajuga, e; *Teucrium*, e; *Lavandula*, e; *Nepeta*, e; *Prunella*, e (new record — one mine with puparium found at Barnet, London); *Galeopsis*, e; *Lamium*, e j; *Leonurus*, e; *Ballota*, e; *Stachys*, e; *Salvia*, e i; **Satureja**, **E**; *Majorana*, e;

Origanum, e; *Clinopodium*, e; *Lycopus*, e; **Mentha**, e i **J**; *Lallemantia*, e; *Molucella*, e; **Bystropogon**, **K**.

Solanaceae

Lycium, **E**; *Hyoscyamus*, e; **Solanum** (incl. *Lycopersicon*), **A C** e i j **N**; *Withania*, i; *Nicotiana*, e; **Petunia**, **A** e i.

Scrophulariaceae

Verbascum, e; *Antirrhinum*, e i k; **Linaria**, a **E** i **N**; *Kickxia*, e; *Chaenorrhinum*, e; *Cymbalaria*, e; *Maurandia* (incl. *Lophospermum*), e; *Collinsia*, e; *Scrophularia*, e; *Mimulus*, e; **Veronica**, **A** i; *Melampyrum*, e (Buhr, 1960); *Rhinanthus*, e (Buhr, 1960).

Plantaginaceae

Plantago, **K** j.

Valerianaceae

Valerianella, e; **Valeriana**, **E**; *Kentranthus*, e.

Cucurbitaceae

Cucumis, e j; *Cucurbita*, e j; *Citrullus*, e.

Campanulaceae

Jasione, e (Vimmer, 1931); *Campanula*, e i.

Compositae

Tubuliflorae

Ageratum, i; *Mikaniopsis*, a; *Aster*, i; **Erigeron**, a **E** i; *Gnaphalium*, i; **Helichrysum**, **E** i; **Inula**, **E**; **Helianthus**, i **M**; **Dahlia**, a **E** i; **Bidens**, **A** i **K**; **Galinsoga**, **A**; *Coreopsis*, i; *Cosmos*, i; *Gaillardia*, i; **Anthemis**, **E**; **Matricaria**, **E**; **Chrysanthemum** (incl. *Tanacetum*), a **E I J N**; **Artemisia**, **E J**; *Cotula*, a; **Senecio**, **E**; **Doronicum**, **E**; *Gynura*, i; *Calendula*, i; **Gazania**, **E**; **Arctium**, **E**; **Carduus**, **K M**; **Cirsium**, **E**; **Centaurea**, **E** i; *Carthamus*, i; *Gerbera*, i.

Liguliflorae

Taraxacum, **E**; **Sonchus**, a **I N**; *Lactuca*, a i; *Launaea*, i.

IV. Notes on types and nomenclature

The first names which appear available for the two widespread species of this group are *Phytomyza syngenesiae* (Hardy) and *Phytomyza horticola* Goureau. I have thought it desirable to designate neotypes of both these species, in order to clarify the application of the names.

Hardy (1849) described his *Chromatomyia syngenesiae* on the basis of Scottish material bred from *Senecio vulgaris*, *S. jacobaea*, *Cirsium arvense*, *Sonchus oleraceus* and *Senecio cruentus* ("*Cineraria*"). His type material is probably no longer in existence (see Basden, 1962). Since he makes no reference to the acrostichal hairs in his description it is likely, as Hendel (1934) suggested, that his concept was composite, including also the *Cirsium*-feeding species *Phytomyza autumnalis* Griffiths (= *affinis* auctt. nec Fallén). However I have little doubt that most of his material belonged to the species for which I propose to use the name in this paper. This species is evidently very common on wild *Senecio* and *Sonchus* in Britain, and there is a confirmed bred specimen from Scotland. A British specimen bred from one of Hardy's original host-plants is hereby designated neotype.

Goureau (1851) stated that his *Phytomyza horticola* fed on diverse garden plants: he obtained specimens from *Cheiranthus cheiri*, *Crambe maritima*, *Tropaeolum majus* and *Papaver somniferum*. I think that the name should be properly applied to the polyphagous species to which I propose to apply it in this paper, since all material which I have seen from Cruciferae, *Tropaeolum* and *Papaver* is referable to this species. Most of Goureau's material is now lost, but there are a few specimens in the possession of Mr. J. E. Collin of Newmarket, Suffolk. These are specimens which Goureau

allowed ROBINEAU-DESVOIDY to retain. Later they were incorporated in the BIGOT collection, which has come into Mr. COLLIN's possession. There is in this collection a single male labelled, presumably by BIGOT, "*Phyt. horticola* Gour. R. Desv. nomt. EX COLL. BIG.", but there is nothing to indicate the host-plant. I have established by dissection that this represents *syngenesiae*. In view of its specific identity I do not believe that it can represent one of the specimens referred to in GOUREAU's original description. But it is clear from ROBINEAU-DESVOIDY's (1851) account of "*Phytomyza geniculata* Macquart" (the name which he applied to GOUREAU's material of *horticola*) that GOUREAU obtained additional material from other host-plants, and a species of Compositae, *Matricaria officinalis*, is included in his list of hosts. It seems likely therefore that the extant specimen labelled as "*horticola*" is not a syntype, but an additional specimen bred after the preparation of GOUREAU's paper (which was originally read at a meeting of the Société Entomologique de France in March, 1848, although not published until 1851). ROBINEAU-DESVOIDY did not examine GOUREAU's material until 1851 (see the footnote added by GOUREAU to the introduction of his paper): there is thus a three-year gap between the preparation of their respective papers although both were published in the same year. In the absence of any syntypes, I am hereby designating a German specimen bred from one of GOUREAU's original host-plants as neotype.

The use of the well-known name *Phytomyza atricornis* Meigen for any of the species treated in this paper seems without any firm justification. MEIGEN's (1838) brief description could equally well apply to a large number of species. The name does not appear to have been used for the species now under consideration before the publication of HENDEL's "Prodromus" (HENDEL, 1920). KALTENBACH (1874) had used it for a miner of *Pimpinella*, probably the species subsequently named *Phytomyza pimpinellae* Hendel. Why HENDEL revived the name is obscure. According to BECKER (1902) no types of *atricornis* are present in either of the collections containing MEIGEN's material (in Paris and Vienna): at my request Dr. A. KALTENBACH has been kind enough to make a further search for type material in Vienna (where is the only MEIGEN material to which HENDEL had access), but without success. It is thus impossible to give any firm opinion on the identity of the original *Phytomyza atricornis* Meigen. In view of the widespread use of this name in recent economic literature it is arguable that it should be conserved by the designation of a neotype or reference to the International Commission on Zoological Nomenclature. I have considered these possibilities carefully, but decided against such action. It seems to me that to ascribe the name *atricornis* arbitrarily to one of the two widespread species treated in this paper would of itself create serious confusion in the indexing of future economic literature. Economic entomologists are sometimes not aware of recent taxonomic revision in all the groups with which they are dealing, and instances of the use of nomenclature which has been discarded in the main taxonomic literature for thirty years or more could easily be quoted. It seems inevitable therefore that papers will appear for many years in which the name *atricornis* is used in an aggregate sense, referring either to *syngenesiae* or to *horticola* or to both. If the use of the name *atricornis* is continued for either of these species, such records of "*atricornis* s. l." will inevitably become confused with records of "*atricornis* s. str." in all indices of the applied literature. But if, as I now propose, the name *Phytomyza atricornis* Meigen is discarded as a nomen dubium, all future papers which do not take account of the division of the former concept of "*atricornis*" into its component species will be recognised as such by their use of the name "*atricornis*", and no confusion in the indexing of the literature will arise.

The name *Phytomyza geniculata* M. Macquart was used for GOUREAU's *horticola* by ROBINEAU-DESVOIDY (1851). GOUREAU (1861) followed him, and the name has subsequently appeared from time to time in the literature for *horticola* and/or *syngenesiae*. It is evident from ROBINEAU-DESVOIDY's remarks that his interpretation of MACQUART's

name was conjectural, and it is impossible to support his opinion because Goureau had sent material of *horticola* to Macquart, who advised him that it appeared to be an undescribed species (Goureau, 1851, pp. 132 and 148). Macquart's (1835) original description of *geniculata* is entirely inadequate, and it seems likely from enquiries made by Mr. K. A. Spencer that no types exist. The name is thus a nomen dubium, and is in any case preoccupied by *Phytomyza geniculata* Brullé (1832), another nomen dubium.

Another of M. Macquart's (1835) names, *Phytomyza nigricornis* Macquart, has also occasionally been applied to *horticola* and/or *syngenesiae* (for instance by Curtis, 1845, and in pre-war Japanese literature). But this interpretation seems without justification. The large size indicated in Macquart's description suggests that he had before him one of the *Phytomyza robustella* group, but a firm interpretation is not possible on the basis of his brief description. In my view the name can only be discarded as a nomen dubium.

Other old names which have sometimes been incorrectly applied to *syngenesiae* and/or *horticola* are *Phytomyza affinis* Fallén (e. g. by French, 1900), *Phytomyza lateralis* Fallén[2] (e. g. by Robineau-Desvoidy, 1851) and *Phytomyza albiceps* Meigen (e. g. by Kaltenbach, 1874 and Watt, 1923). All three names now have a firmly established application to very different species, and Spencer (1965 b) was recently able to confirm the identity of *affinis* and *lateralis* by dissection of the lectotypes.

The reference to "*Phytomyza cucumidis* Macquart" in J. Macquart (1854) (not the same person as the Dipterist Macquart mentioned above) must refer to *horticola*, if the ascription of the larvae to *Phytomyza* was correct. The brief comment given ("J'ai observé les larves minant les feuilles des Melons et y vivant en société") does not seem to constitute an "indication" in accordance with the International Code of Zoological Nomenclature, and I propose therefore to regard the name as a nomen nudum.

No type material of *Phytomyza tropaeoli* Dufour (1857) can be found in the Dufour collection in the Muséum National d'Histoire Naturelle in Paris. Dufour considered that his material represented a distinct species from *horticola* because it lacked two features mentioned in Goureau's description — "vertex à point noir" and the "liseré blanc" bordering the last segment of the abdomen. He appears not to have been aware of Robineau-Desvoidy's (1851) more detailed description of Goureau's material. Neither of the supposed differences is convincing. The first merely reflects an obscurity in Goureau's original description of *horticola*. It is not clear what he meant by the "point noir", and to add to the confusion he uses the plural ("le vertex est cendré à points noirs") in a later description of the same material (Goureau, 1861). The second supposed difference possibly arose because Goureau omitted to state that the "liseré blanc" on the sixth abdominal tergite was a feature of the female. In the male the development of yellow margins on the abdominal tergites is variable (as also on the tergites preceeding the sixth in the female). If Dufour had a male or males before him in which the bands on the abdominal tergites were absent or poorly developed, this might have seemed to him to conflict with Goureau's description. All the material bred from *Tropaeolum* which I have examined represents typical *horticola*, and there is no evidence of the occurrence of any other species on this plant.

Kaltenbach was somewhat confused by the polyphagy of *horticola* and used several names for the species, including three proposed as new. These were *Phytomyza fediae* (Kaltenbach, 1860) bred from *Valerianella locusta; P. linariae* (Kaltenbach, 1862) bred from *Linaria vulgaris;* and *P. pisi* (Kaltenbach, 1864) bred from *Pisum*,

[2] The converse mistake was made by Della Beffa (1940), whose paper on „*Phytomyza atricornis* Meigen" in fact refers to *Napomyza lateralis* (Fallén).

Ononis and *Vicia faba*. I have no information on the existence of any of the relevant types, but it seems clear from the host-plants given that all three names are synonyms of *horticola*.

I have established that *Phytomyza chrysanthemi* Kowarz (in Lintner, 1891) represents the same species as *P. syngenesiae* (Hardy) by dissection of two males (one of which is hereby designated lectotype) from Kowarz's original material of twenty-one specimens which is preserved in the Deutsches Entomologisches Institut.

The holotype of *Phytomyza subaffinis* Malloch (1914), described from Formosa, is unfortunately a female. But I have no doubt that the name should be regarded as a synonym of *horticola*, since both males from Formosa examined belong to this species and it seems unlikely that any other species of this group occurs in the Oriental Region.

Vimmer (1926) described his *Napomyza lactucae* from two flies bred from leaf-mines on *Lactuca sativa* at Brno, Czechoslovakia. Later (Vimmer, 1931) he synonymised the name with *Phytomyza atricornis* Meigen. The female syntype now in Mr. K. A. Spencer's collection represents either *syngenesiae* or *horticola*. Whether the second syntype still exists I have not been able to establish. On present information I am not able to separate females of *syngenesiae* and *horticola*, and am therefore forced to take an arbitrary decision on the synonymy of Vimmer's name. I propose to regard *lactucae* as a synonym of *horticola*, since this species appears to be the commoner in central Europe.

Phytomyza bidensivora Séguy (1951), described from Madagascar, is clearly conspecific with *horticola*, although there is some slight geographical variation in the form of the aedeagus in this and other material from the Ethiopian region (see the comments under my treatment of *horticola* above). There are two specimens (♂, ♀) on the mount labelled as "type". The male is hereby designated lectotype.

Phytomyza farfarella Hendel (1935) was described from material of both sexes collected at Lake Bled in the Jugoslavian Alps. To prevent future confusion some comment here seems needed on the extraordinary errors which have occurred in the labelling of the original material of this species and *P. farfarae* Hendel. A headless specimen labelled "Huflattich" is labelled as the type of *farfarella*, but clearly does not belong to the species which Hendel has described under this name, since the ratio of its costal segments 2 to 4 is 2.2; in any case it is not from the type locality. Possibly this specimen was intended to be the type of *farfarae*, although I hesitate to express a firm opinion on the basis of a headless female. I have examined two females from the original series of *farfarella* (collected at Lake Bled), one of which bore no determination label, but the other bears type labels referring both to *farfarae* and *farfarella!* This specimen I regard as the true type of *farfarella*. The unfortunate confusion can only have arisen through erroneous labelling, since the two species concerned are readily separable on the basis of the costal ratio and there is no confusion of them in Hendel's published descriptions. I am well satisfied that my interpretation of *farfarella* is correct, although if the male from Lake Bled mentioned in the original description is eventually found (Dr. Kaltenbach has unfortunately not been able to trace it) it is desirable that the form of its aedeagus should be checked.

No nomenclatorial comment is required in the case of *Phytomyza lindbergi* Spencer, a good species described by Spencer (1957) from a single male.

V. Relationship of the *Phytomyza syngenesiae* group with other species of *Phytomyza*

The larvae of the *syngenesiae* group pupate within the leaf, forming a very characteristic apomorph type of puparium (fig. 3) which is also found, most probably by

synapomorphy, in certain other groups included in *Phytomyza* (for instance the *robustella* group, the *milii* group and the species associated with *Lonicera* and Gentianaceae, some of which were until recently misplaced in *Napomyza* on account of their retention of the second cross-vein). In all these groups the anterior spiracles of the puparium are bent downwards, so that they project ventrally through the epidermis of the host-plant. HARDY (1849) proposed to include all species with this form of puparium in a separate genus *Chromatomyia*, and I have no doubt that some similar generic concept will be revived when a comprehensive revision of the species now included in *Phytomyza* is eventually possible. (Whether or not the name *Chromatomyia* is available for such a concept may require an Opinion from the International Commission on Zoological Nomenclature, since the same name was proposed by WALKER (1849) for a genus of Ortalidae.)

Within this rather wide concept I think it probable that there is a close affinity of the *syngenesiae* group with the *milii* group (as defined by GRIFFITHS, 1964) and *P. nigra* Meigen. In these species, as in the *syngenesiae* group, the distiphallus does not lie at the apex of the mesophallus or paraphalli, but has been displaced towards their base. The small ejaculatory bulb found in the *syngenesiae* group may also represent an approach towards the condition found in these other species; and the possibility of correlated synapomorphy in the female genitalia is suggested by SASAKAWA's (1961 a) description of minute spermathecae in both "*atricornis*" and *nigra*. However this suggested relationship is at present only put forward as an hypothesis to be tested, since the genitalia of many species with the appropriate type of puparium have not yet been described.

VI. Discussion of evolutionary problems

In the great majority of Agromyzidae, including almost all species of *Phytomyza*, the range of larval host-plants is restricted to a single genus (representing monophagy) or to a group of related genera in the same family (representing oligophagy of the first degree). HERING (1951) and NOWAKOWSKI (1962) have both expressed the view that the polyphagy of "*Phytomyza atricornis* Meigen" is secondary (i. e. that the species was descended from ancestors with a monophagous or oligophagous host range). This conclusion seems to me substantially correct, subject to the revision of the nature of the problem necessitated by the results of this present study. It is now clear that there is not a single polyphagous "*atricornis*", as previous authors thought, but two species with unusually extensive host ranges. One species *(syngenesiae)* attacks most, if not all, genera of Compositae, but only rarely plants of other families: the second species *(horticola)* is truly polyphagous, freely attacking a wide range of dicotyledonous families, as well as a single monocotyledonous genus *(Allium)*. The present study has established that there are also two species with typically restricted host ranges *(farfarella* and *aragonensis)* which can on firm morphological evidence be grouped with the above two species in the monophyletic *syngenesiae* group. This finding gives strong support to the view that the wider host ranges are secondary, and it may be concluded from the host association of *farfarella* (with *Taraxacum* and *Leontodon*) and *aragonensis* (with *Lactuca*) that the ancestor of the *syngenesiae* group was a species associated with a genus or genera of Compositae Liguliflorae.

There is no morphological evidence that the polyphagous species *horticola* is breaking up into host races. The suggestion that monophagous species had split off from "*atricornis*" was first put forward by HERING (1927), when he discovered *horticola* mining *Plantago* and *Carduus* in the Canary Isles. Since at that time these plants were not known as hosts of "*atricornis*" elsewhere, he suggested that the form of "*atricornis*" on the Canaries was less specialised than that in Europe, from which the monophagous species *P. plantaginis* Robineau-Desvoidy and *P. autumnalis* Griffiths

(= *affinis* auctt.) had split off ("abspaltete"). However HENDEL (1935) rejected this hypothesis, as "*atricornis*" had subsequently been found on *Carduus* in Europe, and he did not consider that *plantaginis* could be so closely related to "*atricornis*" as was implied. My genitalia studies have confirmed that *autumnalis* and *plantaginis* are not the most closely related species to the polyphagous *horticola*, and I must therefore support HENDEL's rejection of HERING's hypothesis. The view that "*atricornis*" is splitting into host races was again put forward in a more generalised form by NOWAKOWSKI (1962), who commented that "a considerable variability of the male genital apparatus, certain external morphological features (either presence or lack of *acr*) as well as puparia and mines of *Phytomyza atricornis* Meig. show a secondary food specialization, i. e. the polyphagous species either losing or having already lost a number of oligophagous or monophagous races". However neither *syngenesiae* nor *horticola* are unusually variable species, at least in respect of their adult morphology, and I can only suspect that NOWAKOWSKI's comments are partly the result of comparison of individuals belonging to more than one species of this group.

The picture which seems to me most consistent with the evidence presented in this paper is one of a progressive expansion of host range from an earlier restricted range (similar to that retained by *farfarella* and *aragonensis*), through the wider range retained by *syngenesiae*, culminating in the polyphagy of *horticola*. That these were successive stages of expansion of the host range and that the species with restricted range have not arisen as host races which "split off" from a polyphagous species, is shown clearly by the fact that the host ranges are not vicariant but overlapping: for instance both *horticola* and *syngenesiae* have been bred from *Taraxacum*, as well as the host-specialist *farfarella*, which is entirely inconsistent with any hypothesis that the latter species can have arisen as a sympatric host race which "split off" from a polyphagous ancestor. The experimental data relevent to this problem are limited, but such as they are support the view that the concept of *horticola* put forward in this paper is an interbreeding community. HUSSEY and GURNEY (1962) reported an experiment in which *Cucumis, Dahlia, Tropaeolum, Chrysanthemum* and *Lactuca* were exposed to the same flies (presumably of *horticola*): eggs were laid on all plants, although only relatively few on *Cucumis*. And KURODA (personal communication) informs me that he failed to find differences in host-plant selection for feeding and oviposition among individuals reared from different host-plants in Japan. Part of the explanation of the maintenance of *horticola* as a polyphagous species may lie in its mating habits. Under laboratory conditions both sexes mate frequently throughout their adult life. If the same is the case in the wild, crossing between individuals reared from different larval food-plants must occur frequently and discourage the establishment of strains with a specialised constitution adapted to a single host.

The secondary expansion of host range shown by *horticola* (and to a lesser extent by *syngenesiae*) is of some evolutionary interest. It is commonplace to talk of excessive specialisation as an evolutionary blind alley, which eventually leads to extinction. While this is often the case, it should not be assumed that specialisation is in all cases irreversible. The evolution of the polyphagous *horticola* from ancestors with a much narrower host-range is a striking example of a retreat from specialisation.

It is difficult to make firm deductions concerning the relationships between the species of the *syngenesiae* group, as the morphological differences between them are few, and for some characters (for instance the shape of the mesophallus) it is not clear which conditions are apomorph in relation to the groundplan of the group. The distribution of apomorph and apooec characters shown in fig. 22 clearly implies the convergent evolution either of character 1 (the reduction of the 2nd *ori*) or character 2 (the reduction of the acrostichals). Two alternative hypotheses concerning the phylogeny thus arise, as shown in fig. 23. The principal difference between these alternatives lies in the position of *aragonensis:* under hypothesis 1 this species is considered the

sister-species of the other four species (which are considered synapomorph in respect of character 1), but under hypothesis 2 the species is considered monophyletic with *syngenesiae* and *horticola* (by synapomorphy of character 2).

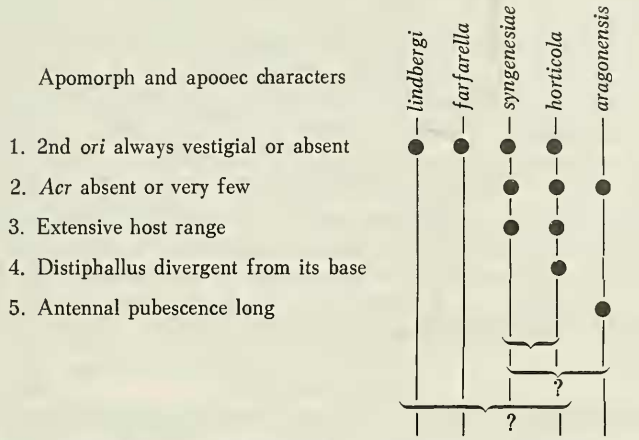


Fig. 22. Relationships between species of the *Phytomyza syngenesiae* group.

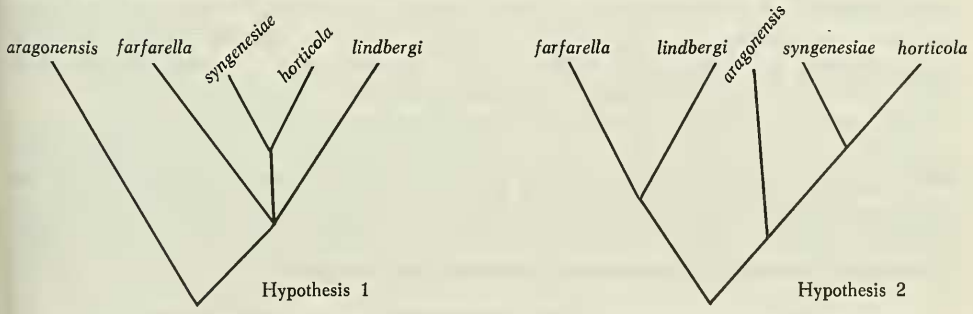


Fig. 23. Alternative hypotheses concerning the phylogeny of the *Phytomyza syngenesiae* group.

It is not yet possible to evaluate the zoogeographical implications of the above phylogenetic hypotheses, for two reasons. First, the information on the distribution of *aragonensis* and *lindbergi* is clearly inadequate; and secondly, puparia of *syngenesiae* and *horticola* are often transported with commercial flower and vegetable crops, with the result that some of the outlying parts of their distribution (e. g. Australia, New Zealand and the Atlantic Islands) may be the result of recent introduction by this means. If *lindbergi* is an endemic species to the Canary Isles, then it may eventually be possible to establish a terminus post quem for its speciation (for a general discussion on the origin of the Dipterous fauna of these islands, see Frey, 1936). The discovery of *aragonensis* and *lindbergi* strongly suggests that interesting results will be obtained from further investigations of the species of the *syngenesiae* group mining Composiate Liguliflorae in the Mediterranean area and the Atlantic Islands. Hitherto all such mines have been assumed to be caused by a single species ("*Phytomyza atricornis* Meigen") and therefore neglected by collectors.

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VIII. Summary

The *Phytomyza syngenesiae* group contains five species, of which two are known to be of economic importance. These are *Phytomyza syngenesiae* (Hardy) (= *chrysanthemi* Kowarz), a species usually attacking Compositae hosts which occurs in Europe, North America, Australia and New Zealand; and *P. horticola* Goureau, a polyphagous species occurring throughout Europe, Asia and Africa. A reliable diagnosis of these species is only possible by dissection of the male aedeagus. In recent literature both species have usually been called "*Phytomyza atricornis* Meigen".

The unusually wide host ranges of the above two species are considered to be secondary. It seems likely that the ancestor of the *syngenesiae* group was associated with Compositae Liguliflorae, on which the occurrence of two host-specialist species in Europe is established. These are *Phytomyza farfarella* Hendel on *Taraxacum* and *Leontodon*, and *P. aragonensis* n. sp. on *Lactuca*. A fifth species of unknown biology, *P. lindbergi* Spencer, is known only from the Canary Isles.

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